

Large Trachycardiinae from the Indo-West Pacific: The group of *Vasticardium orbita* (Broderip & Sowerby, 1833) (Mollusca, Cardiidae)

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Abstract

Two closely related species of Trachycardiinae from the Indo-West Pacific belonging to the *Vasticardium orbita* complex are revised. Young specimens are very similar in shell morphology but adult shells differ in general shape and rib structure. Based on these ontogenetic changes, and also on rib count, which appears to be a stable character, two species are recognised: (1) *Vasticardium orbita* (Broderip & Sowerby, 1833), with a mainly Pacific distribution and four subspecies: *orbita*, *hawaiiensis*, *mendanaense*, and *philippinense* and (2) *Vasticardium luteomarginatum* (Voskuil and Onverwagt, 1991), with a primarily Indian Ocean distribution and three subspecies: *luteomarginatum*, *marerubrum*, and *insulare*, the last of which is herein described as new.

The two species are usually easy to separate, but some specimens are difficult to differentiate. The apparently allopatric distribution of the two species raises the possibility that a single species, with discrete geographical subspecies, is involved.

Introduction

Several Recent species of Indo-West Pacific Trachycardiinae regularly reach more than 80 mm in height, and sometimes can attain 140 mm. The 80 mm limit is reached by large specimens of very few other species in this subfamily, and most species do not reach this size.

The "large" species mentioned above form several groups: the group of *Vasticardium angulatum* (Lamarck, 1819) which has several forms but no defined subspecies (Vidal, 1991); the group of *Vasticardium elongatum* (Bruguère, 1789), with six described subspecies and numerous forms (Vidal, 1993); *Vasticardium fidele* (Vidal, 1992) is similar in shell morphology, but is a little smaller, the largest recorded specimen being only 75.3 mm in height; *Vasticardium papuanum* Vidal, 1996; *Vasticardium gortanii* (Nardini, 1937), a Red Sea fossil species (see below); and the *Vasticardium orbita* (Broderip & Sowerby, 1833) complex, which is examined here.

The present paper, together with the four cited above, concludes a revision of all the known living "large" *Vasticardium* from the Indo-West Pacific.

The most significant conclusion is that young individuals of different species or subspecies of the *V. orbita* complex are very similar in shape, sculpture and ornamentation of the ribs. These characters are different from those found in the other groups of large species of Trachycardiinae. As the shells of juvenile *V. orbita* grow, they are progressively modified so characters differ between juveniles and adults of the same species, as occurs in *V. elongatum* (Vidal, 1993). Using the nature and degree of these changes, and differences in other characters such as shape, colour or rib number, two species are recognised here: *V. orbita* from the Pacific Ocean with four subspecies: *orbita*, *hawaiiensis*, *mendanaense*, and *philippinense* and *V. luteomarginatum*, with a mainly Indian Ocean distribution and

three subspecies: *luteomarginatum*, *marerubrum*, and *insulare*, the last of which is herein described as new.

Details of the synonymy and shell morphology of both species and all of the subspecies are presented below. An alternative viewpoint, based largely on the allopatric distribution of the groups, is that there is a single, variable species. This problem is discussed at the end of the paper.

Materials and methods

Whereas *Vasticardium elongatum* and *V. angulatum* live in sheltered, shallow near shore environments, the available evidence is that *V. orbita* prefers a more exposed outer slope habitat. This explains why the species is relatively scarce in museum collections. Nevertheless, I have been able to examine about 300 specimens in 214 geographically widespread lots, including most of the type material. The ribs have been counted on almost all specimens, and shells of 200 individuals from 132 lots have been measured. The material comes from the following museums: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BISHOP, Bernice P. Bishop Museum, Honolulu; BM(NH), The Natural History Museum, London; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; LACM, Los Angeles County Museum, Los Angeles; MHNG, Muséum d'Histoire Naturelle de Genève, Geneva; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMW, Naturhistorisches Museum, Vienna; NNM, Nationaal Natuurhistorisch Museum, Leiden; QM, Queensland Museum, Brisbane; UGML, University of Guam Marine Laboratory; UMZ, University Museum of Zoology, Cambridge; USNM, National Museum of Natural History, Smithsonian Institution; WAM, Western Australian Museum; ZMA, Zoologisch Museum, Amsterdam; ZMUC, Zoologisk Museum, Copenhagen.

In the subfamily Trachycardiinae numerous shells belonging to different species can have similar combinations of morphometric data (H = Height, L = Length, W = Width), hinge characters, colours, rib number, etc. On the other hand some of these characters, for example rib numbers, vary appreciably intraspecifically or with growth in an individual; to minimise this variability only medium sized individuals were measured. Because of the variability, characters cited above are of minimal use for identifications. Each species possesses a unique and distinctive rib morphology, as opposed to rib number, which allows positive identification. Because of this, rib morphology is used here as the primary criterion for identification and the other characters are used to confirm the identification.

Rib morphology is elaborate in the cardiids examined here, and there are numerous possible combinations and variations. A detailed description would be too long and involved to understand. Accordingly, descriptions have been simplified, and reference is made to the large scale photographs. The descriptions will include two parts: firstly, structure (or profile) of the ribs and secondly, their ornamentation. Rib morphology is further complicated because it differs in various parts of the shell. Two types of variation occur on a single shell. Lateral changes follow the direction of the growth lines. To describe them, the shell will be divided into four quarters: AQ = anterior quarter, MAQ = medio-anterior quarter, MPQ = medio-posterior quarter and PQ = posterior quarter. These changes are often abrupt between MPQ and PQ, but are generally gradual within a quarter or between two adjacent quarters. The PQ, then the MPQ, are the most typical quarters so descriptions begin at the PQ. Secondly, there are changes along the ribs, from the umbo to the ventral margin. To describe these variations, the shell is divided into two parts, a "juvenile" part, corresponding to the early shell near the umbo, and an "adult" part corresponding to the newer shell near the ventral margin. The longitudinal changes are always gradual. Nevertheless, the juvenile sculpture generally remains practically unchanged for the first few centimetres from the umbo. Adult morphology is variable within an individual. The process, or style, of change is constant and becomes an element as important as the morphology itself in the characterisation of the species.

Because of the uniformity of rib morphology within a species it is not necessary to have a lot of material to recognise the presence of a species in a sample of shells, one valve, even a fragment, can be sufficient. Consequently only a few specimens are needed to define new species or subspecies.

Systematics

Family Cardiidae Lamarck, 1809

Subfamily Trachycardiinae Stewart, 1930

Genus *Vasticardium* Iredale, 1927Type species: *Cardium elongatum* Bruguière, 1789; OD Iredale 1927: 75.

Diagnosis: Shell medium to large-sized, ovoid and symmetrical to asymmetrical and posteriorly expanded, obliquely or not, “winged” or truncated. Variably but moderately elongated and inflated. 30–40 ribs, exceptionally 45. Hinge line moderately angled. Cardinal teeth in right valve separated or merely touching at their base and never connected by a high and narrow dorsal saddle. Ribs enlarge quickly in juvenile median and anterior parts, square-sided and fully ornamented, directly following small smooth very early shell. In PQ, ribs always high and square-sided in juvenile shells, always simple, not divided into two parts; top scales or nodules always arranged in a single row along the apex. In other quarters of adult shells, ribs generally high, often squared and overhanging interstices, rarely triangular, often bearing scales or tubercles in MPQ with crenulated margins, cross-bars in anterior half. Interstices rather deep and wide, with a flat bottom, smooth or finely striated independently of flanks of ribs, never hollowed.

Remarks: Three generic names have been utilised for the large Trachycardiinae from the Indo-West Pacific: *Trachycardium* Mörch, 1853 [Type species *Cardium isocardia* Linné; SD von Martens, 1870: 586], *Acrosterigma* Dall, 1900 [Type species *Cardium dalli* Heilprin, 1877; OD], and *Vasticardium* Iredale, 1927. In previous papers (Vidal, 1991, 1992, 1993) I used *Acrosterigma*. However, the subfamily is in need of generic revision, particularly in the Indo-Pacific where some thirty species have not been covered in recent monographs. I have now concluded that *Acrosterigma* is not appropriate for the large Indo-Pacific Trachycardiinae, and follow Iredale (1927) in recognising *Vasticardium*. *Acrosterigma* is now restricted to some American Recent and fossil species and to several smaller Indo-Pacific species.

Group of *Vasticardium orbita* (Broderip & Sowerby, 1833).

Diagnosis: Shell large, often asymmetrical when fully adult; MPQ often transversally expanded, PQ often winged; posterior part rarely appreciably truncated. Lunule large and well delineated with raised margins of shell forming a double wall in its axis. Basement of anterior tooth in both valves characteristically pointed and “hooked” and particularly large and prominent, with a straightened internal limit. In juvenile median and anterior part of the shell, ribs high with subtriangular, slightly rounded smooth top, with edges crenulated by regularly set successive nodules and slightly overhanging interstices which are regularly and finely striated independently of flanks of ribs which are smooth (about two striae versus one marginal nodule); in adult median part, frequent herringbone structures formed by the top rugae.

Remarks: The “hooked” character of the anterior lateral teeth (see examples pl. 1, figs. 2 and 4b or pl. 3, fig. 4b) is a distinctive feature of this group, never present in any other large Trachycardiinae. The rib morphology of the juvenile median part is also very typical of the group.

Vasticardium orbita (Broderip & Sowerby, 1833)*Cardium orbita* Broderip & Sowerby, 1833: 83.

Diagnosis: Shell very large, reaching 125 mm in height, moderately elongated and variably depressed (Table 6). Subequilateral, ribs straight in projection on plane separating both valves (and not curved

Table 1. Comparison of rib morphology of two subspecies of *Vasticardium orbita* (Broderip & Sowerby, 1833).

<i>V. orbita philippinense</i>		<i>V. orbita orbita</i>	
PQ	Ribs low, wide, flat or slightly concave Interstices(i)** thin, narrow Main scales(s) slightly twisted to tubercule, short, or forming thin posterior wall (w) on rib. Anterior marginal thin, slanted scales frequent.	PQ	Ribs high, square-sided, edges overhanging Interstices narrow, deep, flat Main scales almost straight on posterior half of rib top. No anterior marginal scales.
MPQ	Contrast with PQ variable. Ribs low, flat-rounded, rarely slightly overhanging. Interstices very narrow Top main scales AOS* or AT but can be absent. Interstices very narrow, wider onwards. Top main scales = AOS* or AT* frequent, but can be absent. Anterior margin crenulations (cr) present or absent Posterior marginal crenulations (cr) present or absent	MPQ	Contrast with PQ weak. Ribs high, trapezoidal, flat topped, sharp overhanging edges. Interstices narrower than ribs Top scales derived from marginal crenulations sharp edges overhanging. Interstices narrower than ribs. Possible top scales derived from marginal crenulations (= not AOS) Numerous anterior marginal crenulations, oblique, prickly. Strong posterior marginal crenulations oblique, prickly.
MAQ	Ribs medium, rounded to squared becoming sharp-edged onwards.	MAQ	Ribs high, trapezoidal, sharp crenulated edges, top flat.
& AQ	Marginal oblique, crenulations lengthen, form open herringbone and onwards curved rugae.	& AQ	Marginal oblique, crenulations progressively join, form herringbone, then onwards curved rugae.

* AOS, AT: Additional oblique scales (or tubercles): homologous in MPQ of the main top scales of PQ, in addition to the posterior marginal crenulations, but not derived from them. ** i,s,w,cr these initials refer to pl. 3, fig. 1.

backwards). Often "winged" (posterior half of PQ flared out, like a wing); winging often accentuated by a slightly concave radial zone between MPQ and PQ, also detectable in margin. External colour with red brown to purple more or less concentric irregular splashes on a whitish or beige background. Internal margin always coloured in dark purple. Mean rib number 42.2, range 36–50. Rib morphology variable according to the subspecies.

Distribution and subspecies: Four geographical subspecies of *Vasticardium orbita* can be recognised: *Vasticardium orbita orbita* from southeastern Polynesia (Cook Is., Society Is., Tuamotu Is., Pitcairn I.); *V. orbita hawaiiensis* from the Hawaiian Islands; *V. orbita mendanaense* from the Marquesas; and *V. orbita philippinense* from other parts of the tropical western Pacific (Philippines, eastern Indonesia, Papua New Guinea, Micronesia, northwestern Polynesia, Melanesia, northern Queensland and northwestern Australia). *V. orbita* is replaced by *V. luteomarginatum* in the Indian Ocean (Christmas I. and northwestern Australia excepted, see below).

Vasticardium orbita orbita (Broderip & Sowerby, 1833)

Pl. 1, figs. 1, 2, 3a–b.

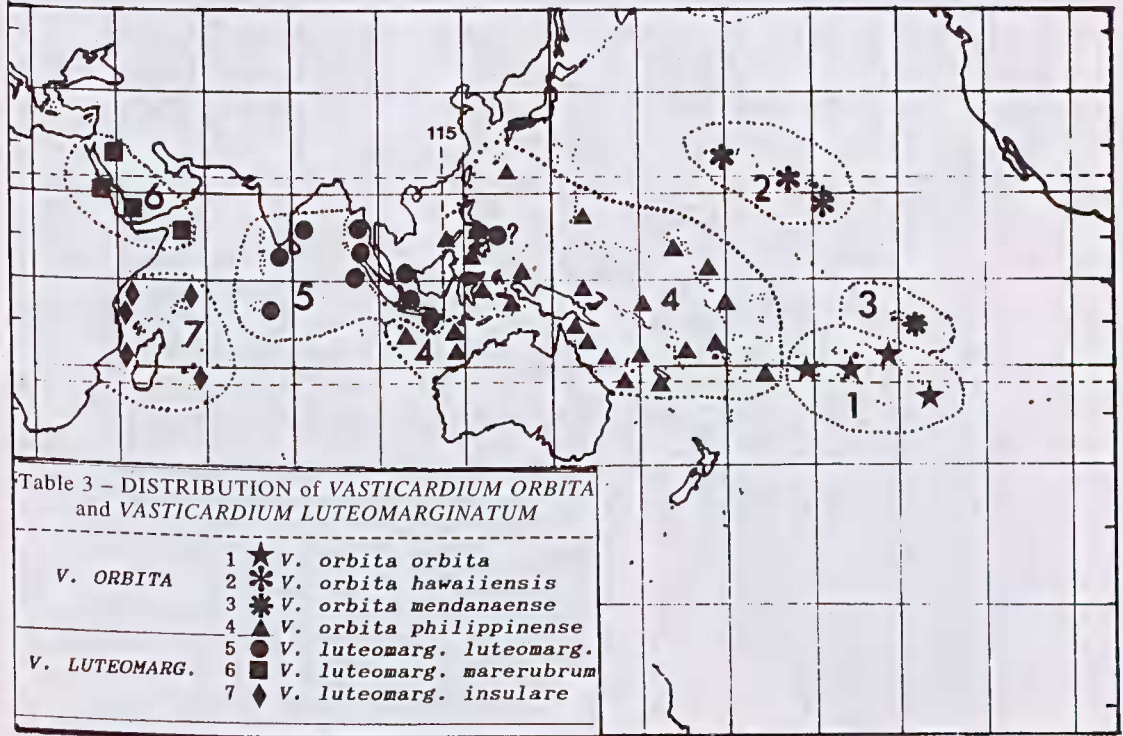
Cardium orbita Broderip & Sowerby, 1833: 83. Sowerby, 1834: fig. 13.

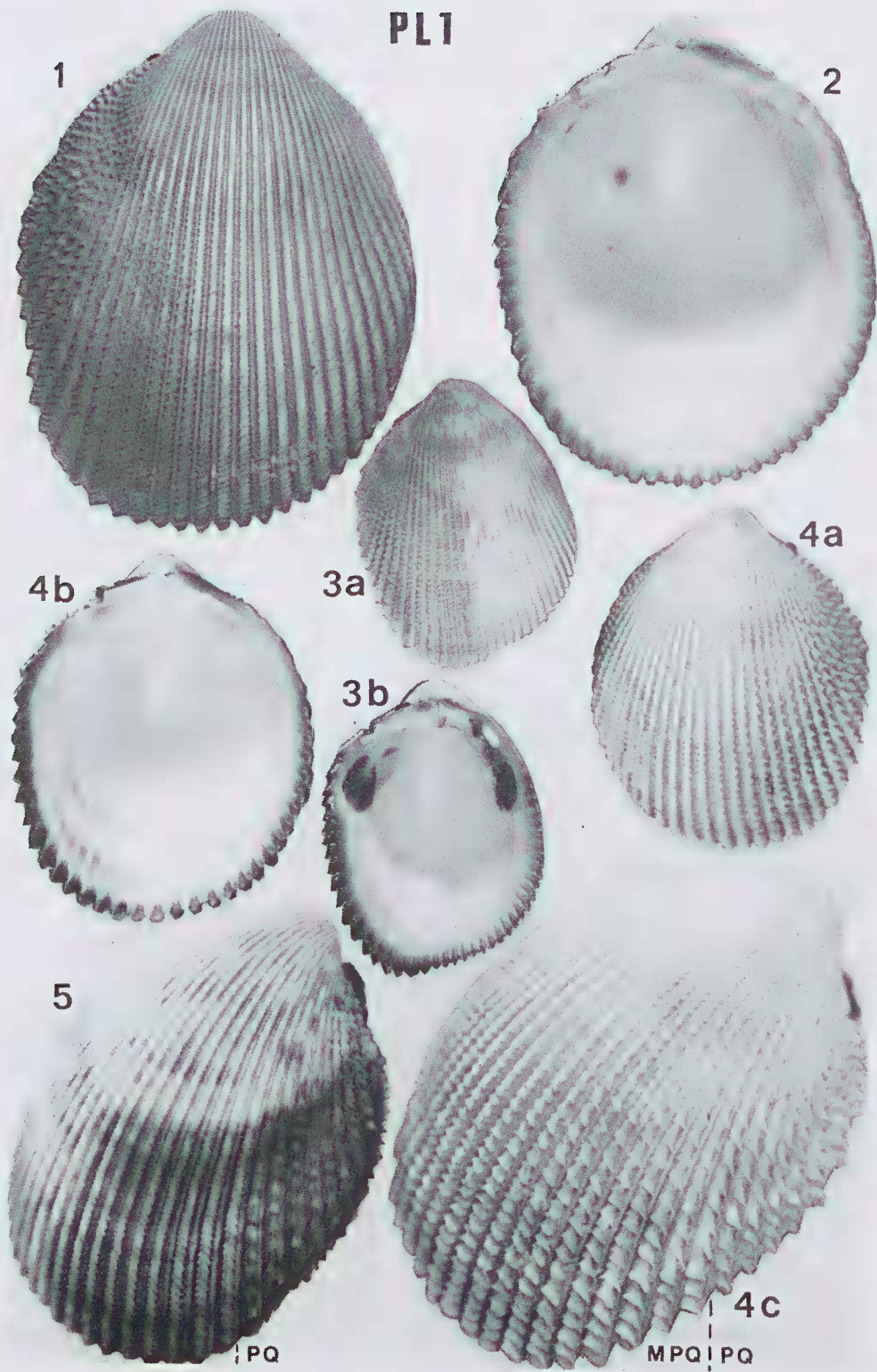
Laevicardium (*Trachycardium*) *philippinense* (Deshayes) Shirley *sensu* Fischer-Piette, 1977: 49, pl. 3, fig. 4 & pl. 4, Fig. 1. [Not *V. orbita philippinense* (Hedley)].

Table 2. Comparison of rib morphology of two subspecies of *Vasticardium orbita* (Broderip & Sowerby, 1833).

<i>V. orbita mendanaense</i>		<i>V. orbita hawaiiensis</i>	
PQ	Ribs very high, flat topped, sharp, edges overhanging. Interstices as wide or wider than ribs. Main scales slightly twisted on most of top. No anterior marginal crenulations, only festoons.	PQ	Ribs slightly high, square-sided, edges rather smooth. Interstices narrower than ribs. Main scales twisted to conical on all of rib top, ventrally straighter. No anterior marginal crenulations festoons rare.
MPQ	Contrast with PQ strong. Ribs very high, asymmetrical, trapezoidal overhanging, rather smooth edges. Interstices wider than ribs. No main scales, top smooth. Numerous anterior marginal crenulations, oblique, prickly. Strong posterior marginal crenulations, oblique, prickly.	MPQ	No contrast with PQ. Ribs high, triangular, flat-top, sharp edges. Interstices as wide as ribs. Top main scales twisted or conical as in PQ (=AOS). Numerous anterior marginal crenulations, oblique, prickly. Numerous posterior marginal crenulations, herringbone with AOS, disappearing.
MAQ	Ribs very high, trapezoidal, sharp, crenulated edges, top flat.	MAQ	Ribs high, round-triangular to squared, edges crenulated.
& AQ	Marginal oblique crenulated, progressively join form herringbone, then onwards curved rugae.	& AQ	Asymmetrical herringbone top rugae become progressively straight then curved.

* AOS, AT: Additional oblique scales (or tubercles): homologous in MPQ of the main top scales of PQ, in addition to the posterior marginal crenulations, but not derived from them.





Types: Three syntypes in BM(NH), Cuming's collection, uncatalogued, from Anaa Island, Polynesia. The largest specimen is figured by Sowerby (1834: fig. 13) and Reeve (1845: fig. 85) and here (pl. 1, fig. 1).

Diagnosis: By far the largest subspecies (height up to 125 mm); adult shell thick and heavy. Young specimens about equilateral and ovoid; fully adult shells less equilateral (a little truncated and winged in PQ), and appreciably elongated (lengthening due to an expansion limited to MPQ, which protrudes in the ventral margin (pl. 1, fig 3a–b)). Colour beige with red-brown to purple splashes more abundant in posterior half, sometimes entirely darker coloured. Mean number of ribs 45.4 (range 41–50). Ribs are straight in projection, sometimes a little curved forwards, even in the largest shells. See Table 1 for rib morphology of adult shell.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Syntypes [BM(NH)]	83.0	64.0	58.3	0.77	0.91	42
	72.5	58.6	48.3	0.81	0.82	45
	38.4	33.4	26.0	0.87	0.78	44
POLYNESIA, Tuamotu [MNHN]	124.4	94.0	86.9	0.76	0.92	46
POLYNESIA, Tuamotu [MNHN]	124.5	92.1	(82.0)	0.74	0.89	46
POLYNESIA, Gambier [MNHN]	121.5	89.9	83.2	0.74	0.93	50
POLY., Tahiti [USNM 879726]	77.4	59.2	(52.6)	0.76	0.89	44
PITCAIRNS [USNM 731901]	81.6	64.0	(53.6)	0.78	0.84	48
COOK, Mauke [UGML BMAK71]	76.1	60.8	(49.0)	0.80	0.81	47
COOK, Rarot. [UGML BRAR118]	69.4	56.6	46.6	0.82	0.82	47

Other specimens:

1 – Morphometric data range: 42.7– 36.3– 27.0– 0.71– 0.74–
(13 measured in 12 lots) 121.2 86.0 85.0 0.89 0.99

2 – Rib counts (18 counted in 15 lots): 41–50

General mean morphometric ratios, shells H over 65.0: 0.78 0.88
(14 measurements in 12 lots) S.D.: 0.034 0.050

General mean rib number (28 counts in 27 lots): 45.4 S.D.: 2.01

Material examined: The type specimens – Other lots: Polynesia: Tahiti : 1(MNHN), 2(USNM); Moorea 1(LACM); Tuamotu: Hao: 1(MNHN); Aratica: 1(MNHN); Anaa: 1(MNHN), 1(ZMA)– Pitcairn: 2(USNM)– Cook: Aitutaki: 4(UGML); Rarotonga: 2(UGML); Mauke: 2(UGML). Pacific Ocean: 2(MNHN), 1(IRSNB), 1(MHNV); No Locality: 2(MNHN), 1(ZMA), 1(AMS), 1(BM(NH)).

Distribution: Three Polynesian ridges: Cook Is., Society Is., and Tuamotu Is.

Remarks: *V. orbita orbita* is distinguished from the other subspecies by its greater number of ribs, shell shape, often its large dimensions and weight. The mean morphometric ratios are different, with the shell more elongated and more globose (Table 6). The shortness of the posterior scales on the ribs in the PQ, and the absence of twisted or conical scales in the MPQ separate it from *hawaiiensis*; *mendanaense* is smaller and more vividly coloured, has higher ribs and wider interstices in the PQ

Plate 1. Figure 1. Syntype of *Cardium orbita* figured by Sowerby. BM(NH). L= 64.0mm. Figure 2. Another syntype of *Cardium orbita*. BM(NH). L= 58.6mm. Figure 3a–b. *Vasticardium orbita orbita*. Very large specimen from Tuamotu Archipelago. MNHN, Coll. Vidal. L= 92.1mm. Figure 4a–c. *Vasticardium orbita hawaiiensis*. Specimen from Kaneohe Bay, Oahu, Hawaii. 4c. PQ and MPQ zones. MNHN, Coll. Burgess. L= 48.0mm. Figure 5. *Vasticardium orbita mendanaense*. Specimen from Nuku Hiva Is, Marquesas, PQ and MPQ zones. MNHN, coll. Vidal. L= 39.1mm.

and MPQ, and only rarely has short oblique scales in the MPQ; *philippinense* differs by rib morphology (in particular *philippinense* usually has numerous AOS or AT in the MPQ combined with separate marginal crenulations which do not exist in the nominal subspecies, where the straight and oblique scales of the MPQ result from the modification of the posterior marginal crenulations).

It is difficult to understand why Fischer-Piette (1977: 30) synonymised *C. orbita* with *C. flavum* Linné.

Vasticardium orbita hawaiiensis (Dall, Bartsch & Rehder, 1938)

Pl. 1, figs. 4a–b–c and pl. 4, fig. 3.

Trachycardium hawaiiensis Dall, Bartsch & Rehder, 1938: 155, pl. 41, figs. 1–4.

Trachycardium orbita (Sowerby, 1833): Kay, 1979: 556.

Type: Holotype USNM 337390, from Keaukaha, Hilo, Hawaii.

Diagnosis: Shell generally medium-sized for group, but some specimens can reach 90mm or more. Shape generally ovoid and roughly equilateral, sometimes mildly asymmetrical. Rarely strongly winged in the PQ. Moderately elongated and globose. See Table 2 for rib morphology of adult shells.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype[USNM337390]	68.5	55.2	44.8	0.81	0.81	42
Kay's 1979 specimen	65.0	53.0	40.0	0.82	0.75	42
Oahu [MNHN]	59.3	48.2	40.0	0.81	0.83	37
Oahu [MNHN]	58.5	48.0	40.0	0.82	0.83	38
Oahu [MNHN]	57.8	45.3	37.2	0.78	0.82	36
Oahu [MNHN]	55.5	46.0	35.1	0.83	0.76	38
Oahu [MNHN]	50.2	42.2	31.0	0.84	0.73	38
Oahu [MNHN]	47.4	38.3	35.3	0.79	0.92	40
Pearl & Herm[USNM428416]	58.7	50.0	42.5	0.85	0.85	43
Midway[USNM428434]	70.0	54.4	49.0	0.78	0.90	41

Other specimens:

1 – Morphometric data	range:	22.5–	19.6–	15.8–	0.76–	0.78–
(13 measured in 13 lots)		91.8	72.8	65.0	0.85	1.03
2 – Rib counts (20 counted in 20 lots):		38–44				

General mean morphometric ratios, shells H over 45.0:
(16 measured in 13 lots)

0.81	0.82
S.D.: 0.02	0.06

General mean rib number (30 counted in 26 lots): 41.0 S.D.: 1.89

Material examined: Lots: Hawaii: 1(NHFW), 2(LACM), 1(BISHOP); Oahu: 2(MNHN), 1(USNM), 8(LACM), 6(BISHOP); Maui: 2(MNHN), 3(LACM), 2(BISHOP), 1(USNM); Kauai: 2(LACM), 1(USNM); Mokuoloc: 1(AMS); Pearl & Hermes Reef: 1(USNM), 3(BISHOP); Midway: 1(USNM), 1(BISHOP); no loc.: 1(MNHN); Other islands: 6(BISHOP).

Distribution: This subspecies is endemic to the Hawaiian Islands.

Remarks: *V. orbita hawaiiensis* is separated from the nominal subspecies by its more regular ovoid shape and smaller number of ribs and from the other subspecies by the presence of wide twisted scales or conical ornamentation both in the PQ and the MPQ of the adults, without any contrast between these two zones.

Pl. 1, fig.5 and pl. 2, figs. 1a-b.

Type: Holotype BM(NH) 1897.4.30.4, from Marquesas, Thomas collection (pl. 2, figs. 1a–b).

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype[BM(NH)1987-4-30-4]	61.2	52.1	45.0	0.85	0.86	39
Marquesas [MNHN]	61.2	49.5	41.5	0.81	0.84	40
Marquesas [MNHN]	63.5	56.2	52.0	0.89	0.93	39
Marquesas,NukuHiva[MNHN]	49.8	42.0	(34.0)	0.84	0.81	39
Marquesas,NukuHiva[MNHN]	46.0	39.1	(30.0)	0.85	0.77	40
Marquesas[ANSP156209]	63.0	52.7	(42.2)	0.84	0.80	40
Marquesas[USNM700277]	51.2	44.8	37.4	0.87	0.83	40
Marquesas[USNM799407]	43.6	36.4	28.3	0.83	0.78	39
Marquesas[USNM790457]	42.7	35.2	(30.0)	0.82	0.85	39
Marquesas[ANSP315633]	40.5	34.7	29.2	0.86	0.84	37

1 - Morphometric data	range:	33.5-	8.0-	22.0-	0.82-	0.73-
(9 measured, in 6 lots)		51.6	43.0	36.0	0.88	0.84

2 - Rib counts (11 counted in 8 lots): 37-43

General mean morphometric ratios, shells H over 40.0:	0.85	0.82
(16 measured in 9 lots)	S.D.: 0.02	0.03

General mean rib number (21 counted in 11 lots): 39.4 S.D.: 1.01

Material examined: The holotype. Other lots: Polynesia: Marquesas: 3(MNHN), 2(ANSP), 1(IRSNB), 3(USNM), 1(LACM), 4(BISHOP).

Distribution: This subspecies is endemic to the Marquesas.

Remarks: *V. orbita mendanaense* is easily separated from *V. orbita orbita* and *V. orbita hawaiiensis* by its smaller dimensions, darker colours, strong contrast between PQ and MPQ. It differs from *V. orbita philippinense* mainly by its high ribs and wide interstices in the posterior half of the shells.

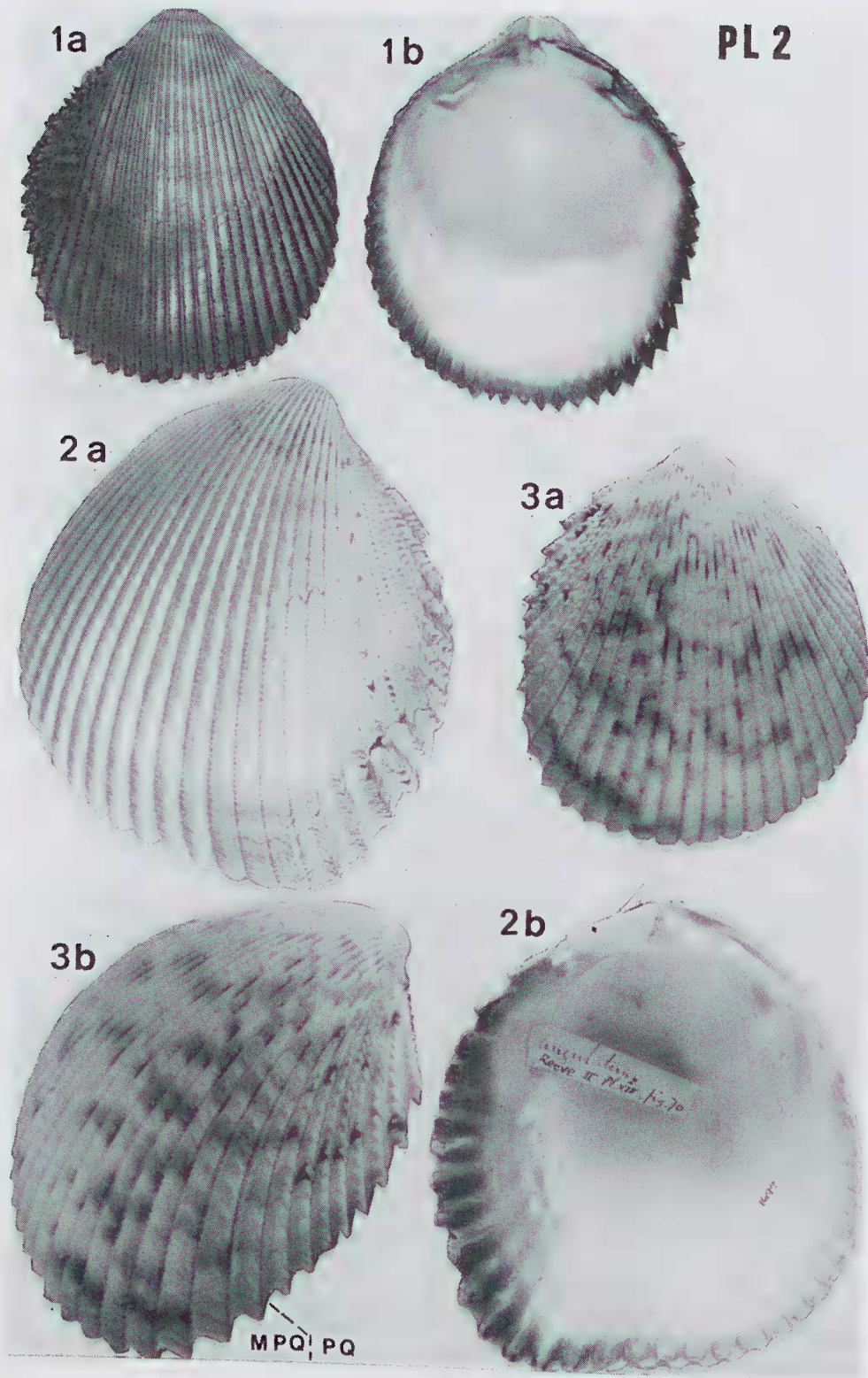
Pl. 2, figs. 2a-b, 3a-b, and pl. 3, figs. 1, 2.

Cardium angulatum Lamarck *sensu* Reeve 1845: Sp. 70, fig. 70. [Not *Cardium angulatum* Lamarck, 1819].

Cardium philippinense Deshayes: Hedley 1899: 503.

Cardium (Trachycardium) pseudoangulatum Bülow, 1905: 79, pl. 1, fig. 3.

Cardium philippinensis Deshayes: Shirley, 1912: 95.



Trachycardium orbita (Sowerby): Wells *et al.* 1990: pl. 78, fig. 368.

Acrosterigma mendanaense (Sowerby) *sensu* Lamprell & Whitehead 1992, pl.29, fig. 188. [Not *V. orbita mendanaense* (Sowerby)]

Types: According to article 72(b) of the Code, the type of *Cardium philippinense* is the shell figured by Reeve as *Cardium angulatum* Lamarck: 1845, fig. 70, UMZ, No 1694, Saul coll., locality unknown (see pl. 2, figs. 2a–b). The type of *C. pseudoangulatum* is the specimen figured by Bülow, not traced, unknown locality; recorded dimensions: H = 95 mm, L = 80 mm, with 38 to 40 ribs.

Diagnosis: Rather large-sized, up to 107.5 mm in height. Shell more or less equilateral, but generally asymmetrical in shape with a straightening in the AQ and a winging in PQ. Another straightening may occur on the ventral margin: its combination with adjacent PQ truncation makes a rough angle in the margin. Reeve's specimen (1845: fig. 70) is abnormally angulated in this way. Moderately elongated, and rather depressed (the most of all subspecies, see Table 6). Colour always beige with brown-purple, irregular, more or less concentric splashes, often darker in interstices, and more abundant in MPQ. In PQ, presence of short squared dark brown stains. Internal margin dark purple, rarely partially yellow. Ribs often straight in projection, even in asymmetric forms, but specimens with an oblique expansion of the MPQ with ribs turning backwards (characters of *Vasticardium luteomarginatum*) occur. See Table 2 for rib morphology of adult shells.

Measurements:	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Type specimen[UMZC1694]	107.3	90.5	70.2	0.84	0.78	36
Philippines[BM(NH),Deshayes]	91.5	78.0	58.0	0.85	0.74	40
Mariana[WAM 3–73]	90.0	73.1	58.0	0.81	0.79	44
Cook, Niue[UGML,BNIUE171]	90.0	72.7	60.8	0.81	0.84	39
Vanuatu, Port Vila[MNHN]	88.4	74.0	58.6	0.84	0.79	39
Solomon [QM]	98.1	84.0	69.3	0.86	0.82	41
PNG, Madang[WAM 40–95]	83.3	70.0	55.7	0.84	0.80	40
N.Qld, Spur Rf[AMSC92097]	102.2	82.5	69.3	0.81	0.84	42
WA, Ashmore Rf[WAM 43–95]	65.0	57.6	39.1	0.89	0.68	40
WA, Christm. Is[AMSC144509]	73.0	59.0	44.6	0.81	0.76	39

Other specimens:

1 – Morphometric data range: 24.4– 20.9– 15.6– 0.74– 0.69–
(61 measured in 43 lots) 107.5 87.3 66.4 0.91 0.87

2 – Rib counts (73 counted in 55 lots): 36–44

General mean morphometric ratios, shells H over 60.0: 0.83 0.78
(44 measured in 30 lots) S.D.: 0.033 0.048

General mean rib number (83 counted in 65 lots): 40.0 S.D.: 2.01

Material examined: The holotype. Other lots: Indonesia: Lombok: 1(ZMA), 1(NNM); Sulawesi: 1(NNM); Moluccas: 2(ZMA); Irian Jaya: 2(ZMA)– Malaysia: Sabah 1(ZMA)– Philippines: 3(LACM), 1(BM(NH)), 2(MNHN), 1(ANSP), 1(MNHN)– Japan: Okinawa: 3(LACM), 1(BISHOP)– Guam: 6(UGML)– Papua New Guinea: Port Moresby: 1(NNM); Hansa Bay: 5(IRSNB)– Solomon: 1(ZMA), 1(LACM), 1(QM)– Marshall: Majuro: 1(UGML)– Kiribati: Tarawa: 1(UGML)– Tuvalu:

Plate 2. Figure 1a–b. Holotype of *Cardium mendanaense*. BM(NH). L= 52.1mm. Figure 2a–b. Holotype of *Cardium philippinense* Hedley [= Shell figured by Reeve (1845: fig 70) as *Cardium angulatum* Lamarck]. UMZ coll. Saul. L= 90.5mm. Figure 3a–b. *Vasticardium orbita philippinense*. Specimen from Cebu, Philippines. 3b. PQ and MPQ zones. MNHN, coll. Vidal. L= 58.0mm.

Funafuti: 1(AMS)– Niue: 4(UGML)– Tonga: 1(BM(NH))– Fiji: 1 (UGML), 1(LACM)– Vanuatu: Port Vila: 1(MNHN), 1(LACM); Malecula 1(MNHN)– New Caledonia: Lifou: 1 subfossil (AMS); Passe de Boulari: 1(Private coll.); Koumac: 1(MNHN); Chesterfield Is: 5(MNHN)– Australia: Queensland and North Queensland: 5(AMS), 2(QM); Swain reef: 1(QM); Western Australia: 1(LACM), 1(IRSNB), 2(WAM); Christmas Is: 1(AMS), 2(WAM). Typical specimens of this subspecies are present in the late Miocene–Pliocene fossil reef of Niue Is. One large bivalve specimen, several valves and fragments, collected by G. Paulay, UGML, have been examined.

Distribution: Intertropical western Pacific Ocean. *Vasticardium orbita philippinense* is totally absent west of 115°East (Christmas I. excepted), where it is replaced by *V. luteomarginatum* (see discussion below).

Remarks: *V. orbita philippinense* differs from the other subspecies primarily in rib morphology (ribs very low and flat, sometimes concave in PQ, with reduced scales and very narrow interstices; ribs low in MPQ with more or less spaced AOS, interstices narrow), and shell morphometry (more depressed, see Table 6).

The name *Cardium philippinense* was first introduced by Hedley (1899: 503), based on several specimens in BM(NH) hand labelled by Deshayes with this name, in synonymy of *C. angulatum* Lamarck, with reference to Reeve (1845, Sp. 70). Reeve's illustration qualifies as an indication under article 12(b)(7) of the Code. More recently, the name *philippinense* has been treated as a valid species by Shirley (1912: 95) and Tomlin (1934: 84), and this action makes it an available name under articles 11(e) and 50(g) of the Code. Accordingly I use the name *philippinense* as the valid name for the western Pacific populations of *V. orbita*. The alternative would have been to use the name *V. pseudoangulatum* (Bülow, 1905), a name that was never used following its publication until it was cited by Vidal (1991) and used by Voskuil & Onverwagt (1991). Considering this very limited usage, there is no reason why the Principle of Priority should not apply. Hedley's usage of the name "*philippinense* Deshayes" is based on material so labelled in the BM(NH). Under articles 9(g) and 50(g) of the Code, Hedley, not Deshayes, is the author of the name.

Vasticardium luteomarginatum (Voskuil & Onverwagt, 1991)

Trachycardium luteomarginatum Voskuil & Onverwagt, 1991: 61, pl. 2, fig. 4 [not figs. 5–6].

Diagnosis: Shell large to very large, reaching 100 mm in length, moderately elongated and rather depressed. Generally inequilateral when adult, with oblique expansion of posterior part and curving of ribs backwards in projection; rarely winged, posterior dorsal margin almost always tilted. Mean rib number 32.5, range 29–36. External colour beige to orange-yellow or pinkish, with darker splashes or stripes, MPQ often darker; internally white with margin strongly coloured yellow-orange, rarely purple. See Table 4 for rib morphology of adult shells.

Distribution and subspecies: Three geographical subspecies of *Vasticardium luteomarginatum* are recognised: *Vasticardium luteomarginatum luteomarginatum* in the northeastern tropical part of the Indian Ocean, Andaman Sea, coasts of Sumatra and Java; *V. luteomarginatum marerubrum* in the Red Sea, Gulf of Aden and northern coast of Somalia; and *V. luteomarginatum insulare* in the southwestern part of the tropical Indian Ocean. The origin of rare isolated specimens from outside this range is considered dubious and needs confirmation (see discussion below).

Remarks: When they described *T. luteomarginatum* as a new species, Voskuil & Onverwagt overlooked or ignored the name *Cardium ignotum* Jousseaume in Lamy 1927. However, this name presents several nomenclatural difficulties, and it is necessary to present here a translation of the paragraph where this name is introduced:

"Born has described (1870, Test. Mus. Caes. Vindob., p. 46, pl. 3, fig. 6–7) *C. leucostoma*, to

Table 4. Comparison of the adult rib morphology of *V. luteomarginatum marerubrum*, *V. luteomarginatum insulare* and *V. luteomarginatum luteomarginatum*.

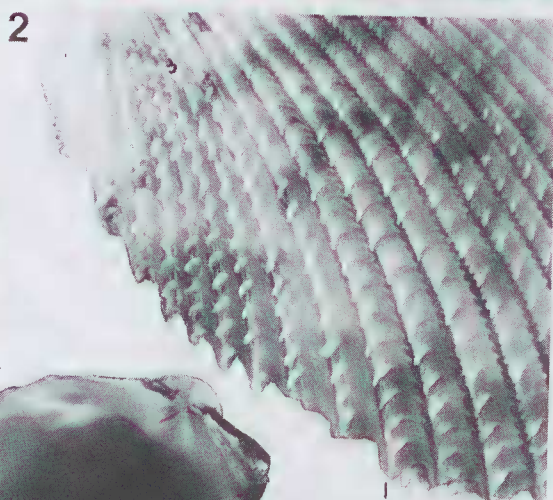
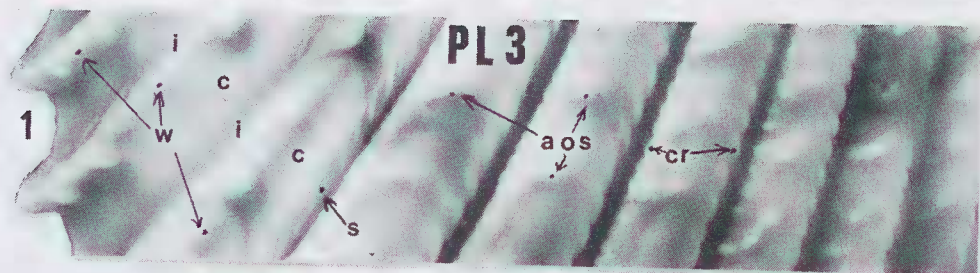
	<i>V. luteomarginatum marerubrum</i>	<i>V.luteomarginatum insulare</i>	<i>V. luteomarginatum luteomarginatum</i>
PQ	Ribs slightly low, wide and flat, edges vary from sharp to smooth. Interstices deep, wide. Posterior main oblique scales long.	Ribs slightly low, wide and flat, edges sharp. Interstices deep, wide. Posterior main oblique scales short.	Ribs very low very flat, sometimes slightly concave, margins smooth. Interstices shallow and very narrow. Posterior main scales very small forming thin strip or scar line.
MPQ	Anterior marginal crenulation persistent. Ribs squared, margin sharp, overhanging. Interstices wide. No AOS* nor AT*. Strong anterior marginal crenulations present. Posterior marginal crenulations present.	Anterior marginal crenulation persistent. Ribs slightly squared, top rounded, margin variable, overhanging or not. Interstices wide. AOS or AT frequent in the whole zone. Anterior marginal crenulations disappearing. Posterior marginal crenulations irregular.	No anterior marginal crenulations. Ribs low, flat-rounded becoming triangular, edges smooth. Interstices narrow, becoming wider. AOS or AT possible, forming a triangular zone in medium aged part. No anterior marginal crenulations. No posterior marginal crenulations
MAQ & AQ	Ribs high, crenulated then onwards top-ridged. Herringbone structure frequent.	Ribs high, crenulated then onwards top-ridged. No herringbone structure.	Ribs high and slightly overhanging, progressively crenulated then top-ridged. No herringbone structure.

* AOS, AT: Additional oblique scales (or tubercles): homologous in MPQ of the main top scales of PQ, in addition to the posterior marginal crenulations, but not derived from them.

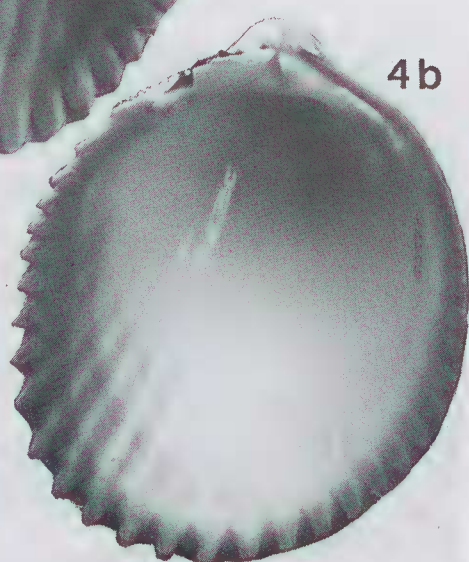
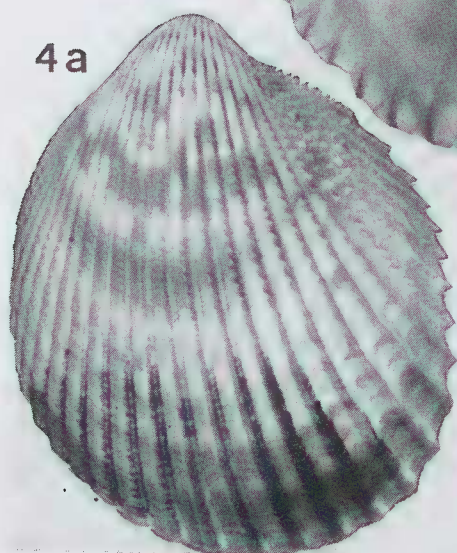
Table 5. Comparison of rib morphology of *Cardium magnum* and *Vasticardium luteomarginatum* (see Pl. 4).

	<i>magnum</i> (fig. 9)	<i>luteomarginatum</i> (fig. 8)
Ribs	Rounded and flattened, margin smooth, in continuity with interstice.	Squared, top flatly triangular, margin crenulated overhanging and independent from interstice.
Interstices	Rounded, regularly grooved, grooves affecting sides of ribs.	Flat, finely striated, striae not affecting sides of ribs.

which he credited Jamaica as locality: although Römer (1869, Conch. Cab., 2d ed., p. 52) thinks this origin is erroneous and that in reality it is the Singapore form figured under this name by Reeve (1845, Conch Icon., pl. IX, fig 47 [This shell really is *T. elongatum*, as indicated by Reeve (see Vidal, 1992: 46)], and pl. XIII, fig. 47). Dr Jousseume says that: “this Indian Ocean species has been confused by authors and is unrelated to the type [of *C. leucostoma*] figured by Born”. He would have proposed for it the name *C. ignotum*, if he had not thought that *C. subrugosum* Sowerby (1840, P.Z.S.L., p. 108; 1841, Conch. Illustr., p. 5, fig. 34; 1844, Reeve, Conch. Icon., pl. XI, fig. 55) might well be, a juvenile of the present species, which would then have to keep that name”. Under articles 11(d) and 15 of the code, a name proposed conditionally before 1961 is available.



PQ | MPQ



References to Reeve provide an indication in the sense of article 12(b)(7) of the code. However, strictly speaking, *C. ignotum* is not even proposed conditionally, since Lamy states that Jousseaume "would have proposed" it [which Jousseaume did not formally do]. Furthermore, Lamy is the only author who has used this name and he treats it as a synonym [of *C. subrugosum*]. Consequently, I treat *Cardium ignotum* as an unavailable name, and use the next available one, viz *T. luteomarginatum*.

Remarks: The differences with the American Atlantic species *C. leucostomum* Born, 1780 (= *C. magnum* L. *sensu* Clench & Smith, 1944), as evidenced by its holotype MHMW 857a, are numerous in rib morphology; only one, which is deciding, will be cited in the median umbonal part of juvenile shells (Table 5 and pl. 4, figs. 8 and 9):

Vasticardium luteomarginatum luteomarginatum (Voskuil & Onverwagt, 1991)

Pl. 3, fig. 4a–b, Pl. 4, figs. 1, 4, 5, 6.

Cardium marmoreum var [2] Lamarck, 1819: 9.

Cardium leucostoma Born: *sensu* Reeve, 1845: Sp. 47, pl. 13, fig. 47. [Not *C. leucostoma* Born, 1780].

Cardium ignotum Jousseaume in Lamy, 1927: 519.

Laevicardium (*Trachycardium*) *enode* (Sowerby) *sensu* Fischer-Piette 1977:62 [Not *Vasticardium elongatum enode* (Sowerby, 1840).

Trachycardium luteomarginatum Voskuil, & Onverwagt, 1991: 61, pl. 2, fig. 4 [not fig. 5–6].

Types: *Trachycardium luteomarginatum*: Holotype NNM 56777, reportedly from Samar Is, Philippines. H= 75.0 mm, L= 61.0 mm, W= 45.5 mm, with 32 ribs (pl. 3, figs 4a–b). Eight individuals cited as paratypes, all from NW Indonesia, all in the NNM: 56578, one specimen, Bay of Batavia; 56579, one left valve, NW Sumatra; 56580, two right valves and one left valve, NW Sumatra; 56581, one left valve, NE Sumatra; 56586, one right valve and one left valve, NW Sumatra. *Cardium marmoreum* var [2]: Lamarck's reference shell MHNG 1085/53, Sri Lanka. *Cardium ignotum*: As seen above the holotype of this nominal species is the shell figured by Reeve (1845, pl. 13, fig 47) from Singapore, not traced.

Diagnosis: Shell large, up to 100 mm in height. Generally slightly asymmetric, with posterior slightly expanded. Sometimes slightly truncated, but very rarely winged, although there is often a slight depression separating PQ and MPQ. Variably but never strongly elongated and moderately depressed (Table 6). In some specimens, tips of interstices in MPQ margin overlap other valve. External colour beige to orange-yellow or pinkish, with darker splashes or stripes, MPQ often darker. Internally white with margin strongly coloured yellow-orange, rarely purple. Ribs almost always curved backwards in projection. See Table 4 for rib morphology of adult shells.

Plate 3. Figure 1. *Vasticardium orbita philippinense*. Same specimen as in Plate 2, figures 3a–b, right valve; detail of PQ and MPQ zones. Scale = x 4.25. (Explanation of abbreviations is in Table 1). Figure 2. *Vasticardium orbita philippinense*. Specimen from Passe de Boulari, New Caledonia; detail of PQ and MPQ zones. Private coll., Nouméa. L= 53.7mm. Figure 3a–b. Holotype of *Trachycardium marerubrum*. NNM. L= 62.0mm. Figure 4a–b. Holotype of *Trachycardium luteomarginatum*. NNM. L= 61.0mm.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype [NNM 56577]	75.0	61.0	45.5	0.81	0.75	32
LamarckType[MHNG1085-52]						
<i>C. marmoreum</i> var.[2]	74.0	62.6	47.7	0.85	0.76	32
Indian Ocean [MNHN]	87.5	71.1	59.0	0.81	0.83	35
India [MNHN]	90.5	77.0	(61.0)	0.85	0.79	30
Andaman Sea [MNHN]	85.0	69.5	53.9	0.82	0.78	34
Thailand, PhuketIs[MNHN]	84.4	70.0	54.7	0.83	0.78	34
Singapore [MNHN]	86.9	68.1	51.5	0.78	0.76	32
Singapore [MNHN]	61.3	53.1	40.5	0.87	0.76	35
Chagos,PBanhos[BMexp1978]	100.0	77.5	60.1	0.77	0.78	34
Chagos,Spur Rf.[UGML]	81.0	65.8	59.1	0.81	0.90	34

Other specimens:

1 – Morphometric data range: 44.6– 39.0– 27.8– 0.79– 0.70–
(13 measured in 7 lots) 90.0 71.0 53.0 0.86 0.83

2 – Rib counts (33 counted in 23 lots): 31–35

General mean morphometric ratios, shells H over 60.0: 0.82 0.78
(21 measured in 13 lots) S.D.: 0.028 0.039

General mean rib number (43 counted in 33 lots): 32.7 S.D.: 1.43

Material examined: The holotype and the height paratypes of *T. luteomarginatum* in the NNM- Other lots: No location 1(MNHN), 1(ZMA), 2(BM(NH))– Indian Ocean 1(MNHN), 1(IRSBNB), 1(MHNV)– Chagos: 1(MNHN), 1(BM(NH)), 2(UGML)– India: 1(MNHN); Sri Lanka: 1(MHNV), 1(LACM), 1(BM(NH))– Nicobar: 1(NMW)– Thailand: Andaman Sea 1(MNHN); Phuket 2(MNHN), 1(LACM)– Singapore: 2(MNHN), 1(BM(NH)), 1(MHNV)– Indonesia: N. Sumatra 1(ZMA); Sabang Is 2(ZMA); Bay of Batavia 2(ZMA); W. Java 1(ZMA); Bali 1(ZMA).

Distribution: *V. luteomarginatum luteomarginatum* totally replaces *V. orbita philippinense* to the west of 115°E (Christmas Island excepted).

Remarks: *V. luteomarginatum luteomarginatum* differs from the two other subspecies by its smoother character, colouration, and rib morphology in the MPQ (ribs rounded to triangular, instead of square-sided). Adult shells are also generally larger.

Vasticardium luteomarginatum marerubrum (Voskuil & Onverwagt, 1991)

Pl. 3, figs. 3a–b and pl. 4, fig. 2.

Cardium rugosum Lamarck *sensu* Reeve, 1845: Sp. 68, fig. 68. [Not *Cardium rugosum* Lamarck, 1819].

Cardium magnum Chemnitz *sensu* Issel, 1869: 74. [Not *Cardium magnum* Linné *sensu* Chemnitz, 1782 = *Cardium angulatum* Lamarck, 1819].

Cardium ignotum Jousseaume in Lamy, 1927: 519.

Cardium subrugosum Sowerby *sensu* Lamy, 1927: 519.[Not *Cardium subrugosum* Sowerby, 1838].

Cardium (Trachycardium) flavum Linné *sensu* Abrard, 1942.[Not *Cardium flavum* Linné, 1758].

Trachycardium marerubrum Voskuil & Onverwagt, 1991: 59, pl. 2, fig. 4 [not fig. 5–6].

Trachycardium enode (Sowerby, 1840) *sensu* Oliver, 1992: 126, pl. 23, figs. 5a–b.[Not *Vasticardium elongatum enode* (Sowerby, 1840)].

Types: *Trachycardium marerubrum*: Holotype NNM 56424, from S. of Giftun Is, Red Sea, Egypt (pl. 3, figs. 3a–b). Ten individuals cited as paratypes, all from the Red Sea, Egypt. Nine are in private collections, only one in the NNM 56573, one right valve.

Diagnosis: Shell medium to large-sized, reaching 93.6 mm in height, generally thick and heavy. Almost equilateral, with often a small expansion of posterior part, and with a slight curvature of ribs backwards in projection. Variably but never much elongated; variably depressed (Table 6). External colour light, white to beige, occasionally with diffuse yellowish to light brown splashes. Interior white, posterior margin white to yellowish, rarely purple. See Table 4 for rib morphology of adult shells.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype [NNM 56424]	73.5	62.0	44.9	0.84	0.72	32
Egypt, Aqaba Gulf[MNHN]	60.1	50.2	(38.0)	0.84	0.76	32
Egypt, Suez Gulf fos[MNHN]	69.2	57.0	(44.0)	0.82	0.77	34
Saudi Arabia, N.Duba[NMW]	93.6	75.5	61.7	0.81	0.82	32
Eritrea, Dahlac Is[MNHN]	71.5	58.5	(48.0)	0.82	0.82	33
Yemen, Perim Is[MNHN]	77.3	63.6	50.0	0.82	0.79	32
Red Sea,unloc.[BMNH1994–088]	72.0	59.2	50.7	0.82	0.86	32
Red Sea,unloc.[MNHN]	75.5	61.2	49.6	0.81	0.81	32
Somalia,Socotra Is[MNHN]	84.1	68.6	49.2	0.82	0.72	32
N.Mogadis[ANSP295813]	59.7	49.0	(37.2)	0.82	0.76	31

Other specimens:

1 – Morphometric data range: 47.5– 39.7– 34.0– 0.79– 0.72–
(26 measured in 9 lots): 81.2 67.5 52.0 0.90 0.85

2 – Rib counts (28 counted in 11 lots): 30–35

General mean morphometric ratios, shells H over 55.0: 0.83 0.78
(32 measured in 16 lots) S.D.: 0.025 0.041

General mean rib number (38 counted in 18 lots):32.4 S.D.: 1.02

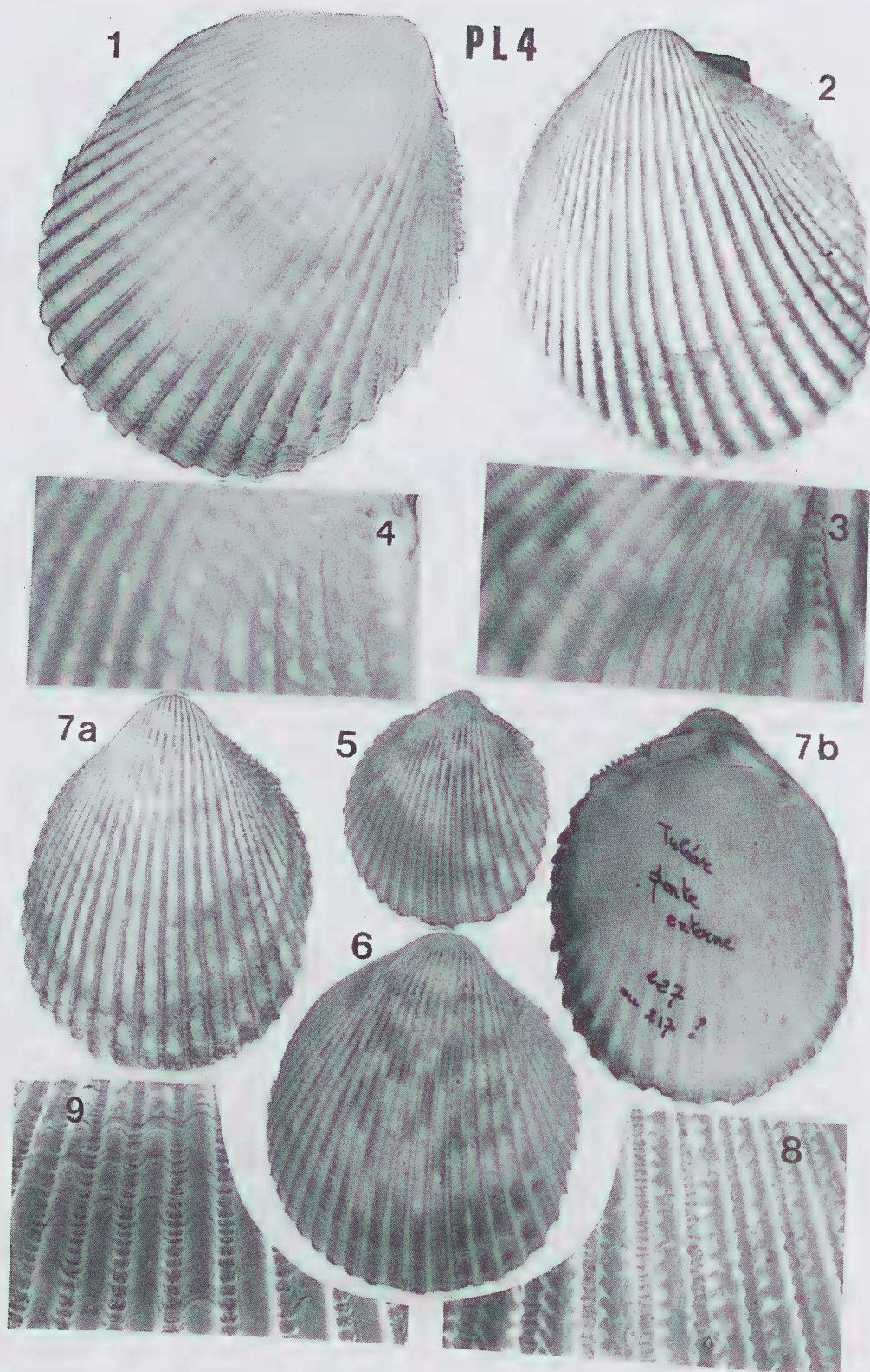
Material examined: The holotype and one paratype of *T. marerubrum* in the NNM. Other lots: Red Sea: 3(MNHN), 4 fossil (MNHN); Gulf of Suez: 1(MNHN)– Egypt: Gulf of Suez: Raz Dib: 1 fossil (MNHN), Sharm el Bahari: 1 fossil (MNHN); Gulf of Aqaba: Gesireh Faraun: 1(MNHN)– Jordan: S. Aqaba: 1(MNHN)– Saudi Arabia: Abulatt Is: 1(MNHN); N. Duba 1(NMW)– SUDAN: Port Sudan: 1(NNM)– Ethiopia: Dahlak Archipelago: 1(MNHN)– Djibouti: Perim Is: 1(MNHN)– Somalia: Abd el Kuri Is: 1(MNHN); Socotra Is: 1(MNHN); N. Mogadishu 1(MNHN).

Distribution: This subspecies is restricted to the Red Sea, southern coast of the Gulf of Aden, and northeastern coast of Somalia. Also present in the Pleistocene raised beaches of the Red Sea.

Remarks: *Vasticardium luteomarginatum marerubrum* differs from the other two subspecies by its lighter colours, outside and inside, by its rugose shell, greater pedomorphic character and the absence of AT and AOS. From the subspecies *insulare* it differs also by not having a purple coloured internal margin.

The light colours and the rugose aspect of this subspecies explain the erroneous identifications as *flavum*, *rugosum*, and *subrugosum*.

Nardini (1937: 253, pl.17, fig.1 and 2a–b) describes both *C. rugosum* and *C. rugosum* var.



gortanii, from the Pleistocene deposits of the Dahlak Archipelago and Port Sudan. *C. rugosum* is a misidentification of *V. luteomarginatum marerubrum*, as several authors do, but *var. gortanii* has little to do with this species, and represents a valid species, *Vasticardium gortanii* (Nardini, 1937). Many specimens of this species, always Pleistocene fossils, are present in the MNHN, mainly in Plaziat's collection from the southern part of the Gulf of Suez in Egypt, but also from Abulatt Is and Museri Is (Calypso expedition, 1951–52). This fossil species, reaching 100 mm in height, belongs to the "large" *Vasticardium*, but not to the *orbita* group. The most significant differences are that it lacks the characteristic "hooked" anterior laterals and the juvenile rib morphology is closer to *V. elongatum*. Although size, general shape, rib number (range 27–32), are equivalent to those of *V. luteomarginatum*, these two species also differ in several other characters, particularly in the rib morphology of adult PQ and MPQ. As far as I know, this remarkable shell has never been found alive, but being a relatively recent fossil, relict populations could still exist in the Red Sea, or elsewhere.

Vasticardium luteomarginatum insulare subsp. nov.

Pl. 4, figs. 7a–b and 8.

Cardium orbata Reeve (sic) *sensu* Dautzenberg, 1929:382 [Not *Cardium orbata* Broderip & Sowerby, 1833].

Types: Holotype, MNHN, a left valve from Madagascar, Tulear area, Thomassin's diving 1969, sta. 227. Paratype No 1, MNHN, a specimen from Zanzibar, coll. Rousseau. Paratype No 2, MNHN, a right valve from Réunion, coll. Vidal. Paratype No 3, MNHN, a specimen from Mauritius, coll. Carrié. Paratype No 4, AMS C67318, a specimen from Mauritius, coll. Ward.

Diagnosis: Smallest subspecies, never reaching 80 mm in height. Practically equilateral, with rarely a small expansion of posterior part or a slight winging, and generally a very slight curvature of ribs backwards in projection. Never very elongated; moderately depressed (Table 6). External colour beige to yellowish with reddish splashes; MPQ often more coloured. Internal colour white, margin always purple, sometimes purple and yellow. See Table 4 for rib morphology of adult shell.

Plate 4. Figure 1. *Vasticardium luteomarginatum luteomarginatum*. Specimen from Singapore close to Reeve's pl. 13, fig. 47. MNHN. L= 87.6mm. Figure 2. *Vasticardium luteomarginatum marerubrum*: Specimen from Perim labelled by Jousseume as *Cardium ignotum*. MNHN, coll. Jousseume. L= 63.6mm. Figure 3. *Vasticardium orbata hawaiiensis*. Specimen from Pearl & Hermes Reef, USNM 428416; detail of the rib sculpture in juvenile PQ, at ligament level. Scale: x 3.5. Figure 4. *Vasticardium luteomarginatum luteomarginatum*. Specimen from the Andaman Sea, MNHN; detail of the rib sculpture in juvenile PQ, at ligament level. Scale: x 3.5. Figure 5. *Vasticardium luteomarginatum luteomarginatum*: Specimen from the Andaman Sea (same as in fig. 4), MNHN coll. Vidal. L= 38.8mm. Figure 6. *Vasticardium luteomarginatum luteomarginatum*. Specimen cited from Swain Reef, Queensland. AMS C303668. L= 56.5mm. Figure 7a–b. Holotype of *Vasticardium luteomarginatum insulare* subsp. nov. MNHN, coll. Thomassin. L= 52.0mm. Figure 8. *Vasticardium luteomarginatum insulare*. Specimen from Ambatoloaka, SW-Nosy Be, Madagascar; detail of the median umbonal sculpture. MNHN, von Cosel coll. Scale: x13.5. Figure 9. *Trachycardium magnum* Linné *sensu* Clench & Smith, 1944. Specimen from Bay of Portobello, Panama; detail of the median umbonal sculpture. MNHN, coll. Vidal. Scale: x25.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype [MNHN]	67.2	52.0	(43.0)	0.77	0.83	32
Paratype 1 [MNHN]	70.2	59.7	43.1	0.85	0.72	32
Paratype 2 [MNHN]	63.0	52.1	(43.0)	0.83	0.83	35
Paratype 3 [MNHN]	65.5	53.5	41.5	0.82	0.78	32
Paratype 4 [AMS C67318]	62.0	49.4	39.4	0.80	0.80	34
Zanzibar [MNHN]	80.0	63.2	(48.0)	0.79	0.76	31
Zanzibar [MNHN]	64.9	53.5	(40.0)	0.82	0.75	29
Mauritius [MNHN]	56.8	48.0	35.8	0.85	0.75	34
Seychelles [BMNH, Winwork]	71.2	58.0	44.1	0.81	0.76	33
Doubt. loc. [AMS C14067]	78.6	67.0	48.2	0.85	0.72	32
Other specimen:	49.0	41.9	29.4	0.86	0.70	33
General mean morphometric ratios, shells H over 50.0: (10 measured in 9 lots)				0.82	0.77	
				S.D.: 0.026	0.040	
General mean rib number (11 counted in 9 lots): 32.6				S.D.: 1.342		

Material examined: The type series – Other lots: Seychelles 1(BMNH), 1(IRSNB)– Mauritius 1(LACM), 1(BMNH), 3(AMS), 2(IRSNB)– Madagascar: 2(MNHN)– Kenya: Shimani 1(MNHN)– Zanzibar: 1(MNHN), 1(LACM).

Distribution: Restricted to the southwestern tropical islands of the Indian Ocean, and the East African coast.

Remarks: *V. luteomarginatum insulare* differs from the other two subspecies in its smaller size, purple internal margin, and often by the presence of well developed AT and AOS. It differs from the nominal subspecies by the more pedomorphic rib morphology. *V. luteomarginatum insulare* is among the three subspecies of *V. luteomarginatum*, the one that most resembles certain medium-sized forms of *V. orbita*, particularly in the subspecies *philippinense*.

Table 6. Comparison of mean morphometric ratios and rib numbers of subspecies of *Vasticardium luteomarginatum* and *V. orbita*.

	<i>Vasticardium luteomarginatum</i>			<i>Vasticardium orbita</i>			
	<i>marerubrum</i>	<i>insulare</i>	<i>luteomarginatum</i>	<i>philippinense</i>	<i>orbita</i>	<i>mendanaense</i>	<i>hawaiiense</i>
L/H	0.83	0.82	0.82	0.83	0.78	0.85	0.81
W/L	0.78	0.77	0.78	0.78	0.88	0.82	0.82
Ribs	32.4	32.6	32.7	40.0	45.4	39.4	41.0

Discussion: *Vasticardium orbita* and *V. luteomarginatum*: species or subspecies?

As discussed, *Vasticardium orbita philippinense* totally disappears to the west of 115°E (Christmas Island excepted) and is replaced by *V. luteomarginatum luteomarginatum*. However, a few specimens of *V. luteomarginatum luteomarginatum* are reported as coming from the east of this line; they are:

- 1) A specimen labelled from New Caledonia, AMS C14067, old collection, H= 78.6 mm, with 32 ribs, is close to the subspecies *insulare*.
- 2) A specimen labelled from Ticao, Philippines, de Burgh's collection BM(NH), H= 63.6 mm, with 34 ribs, is identical to forms of *V. luteomarginatum luteomarginatum* from Singapore.
- 3) A specimen indicated as coming from Swain Reefs, Queensland, AMS C303668, figured by Lamprell & Whitehead (1992: fig. 187) as *Acrosterigma luteomarginata*, H= 65.0 mm with 35

ribs (see pl. 4, fig. 6). This shell, similar to a form of *V. luteomarginatum luteomarginatum*, is the only aberrant record in the Coral Sea, where all other shells of the group, including those from Swain Reef, are *V. orbita philippinense*.

The above three specimens are from old collections, and their presence in an unexpected locality may be due to inadvertent subsequent mixing of lots. Less likely, they could be individual variants of *V. orbita philippinense* with a smaller rib number. The problem is compounded by the stated locality of the holotype of *V. luteomarginatum* being Samar Island, Philippines (with seven specimens in private collections and not seen). This shell is so identical to the Andaman Sea specimens and to some paratypes from Sumatra (zone with AOS and AT only in the medium aged part of the shell, forming a triangle with its apex onwards), that its presence in the Philippines, not previously reported, needs confirmation. According to R. Voskuil (personal communication) this lot originated from a dealer, so an erroneous locality is not impossible.

If the unlikely records are not confirmed, the two species *V. luteomarginatum* and *V. orbita* would be completely allopatric. In view of their many similarities could all forms be considered to be subspecies of *V. orbita*? More observations are needed to solve this problem, but it is considered here to be preferable to separate them at the species level.

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